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DOI: https://doi.org/10.1086/706449

Int. J. Plant Sci. 181(3):000–000. 2020.

1058-5893/2020/18103-00XX$15.00 DOI: 10.1086/706449

# INFLORESCENCE STRUCTURE IN LAURALES—STABLE AND FLEXIBLE PATTERNS

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*Editor: Maria von Balthazar*

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*Pivotal results*. There are recurrent branching patterns. Botryoids, thyrsoids, and compound botryoids and thyrsoids are the most common forms. Panicles, racemes, and thyrses are rare. Panicles and racemes occur in some highly nested Lauraceae and thyrses in Hernandiaceae. Thus, the presence of thyrso-paniculate inflorescences is not characteristic for Laurales, in contrast to the statement by Weberling.

*Conclusions*. An evolutionary interpretation is still difficult because the existing molecular phylogenetic analyses are not fine grained enough and also because the previous phylogenetic results are not robust enough to make firm conclusions within the order. However, the present structural results show that there are trends of occurrence of certain patterns in families or subclades within families, and these may be useful in a morphological matrix of magnoliids (see work by Doyle and Endress for basal angiosperms).

*Keywords:* inflorescences, systematics, basal angiosperms, magnoliids, Laurales, Atherospermataceae, Calycanthaceae, Gomortegaceae, Hernandiaceae, Lauraceae, Monimiaceae, Siparunaceae.

## Introduction

In attempts to study morphological features for a phylogenetic analysis in basal angiosperms and for understanding evolutionary trends, inflorescences have not been explored in detail. Only more recently have inflorescences received attention by evo-devo workers (Benlloch et al. 2007; Prusinkiewicz et al. 2007; Koes 2008). There has been much confusion in the literature with the use of terms in inflorescence morphology. This is discussed in an outline of a current classification based on the work by W. Troll and later authors (Endress 2010).

In basal angiosperms (ANITA grade and magnoliids) there are some comparative studies at the family level including inflorescence structure (e.g., Chloranthaceae: Endress 1987*a*; Eklund et al. 2004; Hernandiaceae: Kubitzki 1969; Lauraceae: Mez 1889; Weberling 1985; Rohwer 1993*a*; Kurz 2000; Myristicaceae: de Wilde 1991; Aristolochiaceae: González 1999; Lactoridaceae: González and Rudall 2001; Piperaceae: Tucker 1982; Remizowa et al. 2005; Sokoloff et al. 2006; Saururaceae: Rohweder and Treu-Koehne 1971; Tucker 1981) and even a preliminary survey of "primitive" angiosperms (Weberling 1988). However, the level in between—the order level—has not been focused on. We provide here new information on inflorescences for all families of Laurales, with an evolutionary perspective where possible. One of the goals is to enlarge the database for a morphological cladistic analysis of basal angiosperms that was started 20 years ago (see Doyle and Endress 2000) and has been repeatedly updated since and used in a number of publications by Doyle and Endress (most recently 2018) and other authors. Weberling (1985, 1988) describes Lauraceae inflorescences in general terms used for angiosperms, emphasizing the overall diversity. In contrast, we try to trace specific features within families, groups of families, and the entire order Laurales. Extant Laurales apparently consist of three major clades. A first clade is the family Calycanthaceae, which appears as sister to all other Laurales (Qiu et al. 1999, 2005; Renner 1999, 2004; Doyle and Endress 2000; Hilu et al. 2003; Massoni et al. 2014). A second clade is formed by Atherospermataceae, Gomortegaceae, and Siparunaceae, with Atherospermataceae plus Gomortegaceae sister to Siparunaceae (Qiu et al. 1999; Renner 1999, 2004; Doyle and Endress 2000; Renner and Chanderbali 2000; Massoni et al. 2014). A third clade is formed by the families Hernandiaceae, Lauraceae, and Monimiaceae, but the phylogenetic relationships between these families have been controversial. They appear in all three possible topologies: Lauraceae sister to Hernandiaceae plus Monimiaceae (Qiu et al. 1999; Hilu et al. 2003), Monimiaceae sister to Lauraceae plus

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*Manuscript received April 2019; revised manuscript received June 2019; electronically published January 13, 2020.*

Hernandiaceae (Doyle and Endress 2000; Chanderbali et al. 2001), or Hernandiaceae sister to Lauraceae plus Monimiaceae (Renner 1999, 2004; Renner and Chanderbali 2000; Qiu et al. 2005; Massoni et al. 2014).

It appears important to document the prominent features (fig. 1) for all seven families. What features may be ancestral in inflorescences of families, groups of families, and the entire order Laurales? It would be interesting to know whether relatively large flowers and few-flowered inflorescences are primitive in Laurales or how many times large flowers evolved from small ones in Laurales. However, this is not yet possible to deduce from the published data. Relatively large flowers and few-flowered inflorescences are known from all Calycanthaceae–Calycanthoideae, some Atherospermataceae (*Atherosperma*, *Laurelia*), and some Monimiaceae (*Tambourissa*). Preliminary screening of inflorescences through the families of Laurales showed the following features of interest (and they serve as a guideline for the presentation of the results):

1. Number of branching orders (*a*) in an inflorescence (unbranched; this is in one-flowered inflorescences); (*b–d*) with branches of first order, such as in botryoids: (*b*) triad; (*c*) five-flowered botryoid; (*d*) seven-flowered botryoid; (*e*) with branches of second order, such as in thyrsoids with triads as lateral units or in compound (double) botryoids; and so on (fig. 1.1).
2. (*a*) Opposite versus (*b*) nonopposite branching (fig. 1.2).
3. Symmetry of branching: presence of (*a*) two (symmetric) versus (*b*) only one (asymmetric) side branch of the same order in a branching system (fig. 1.3).
4. (*a*) Presence versus (*b*) absence of prophylls in the branches of the highest order (outermost branches) (fig. 1.4).
5. Position of prophylls if hypopodium is variously extended: (*a*) basal versus (*b*) at midlength versus (*c*) distal (fig. 1.5).
6. (*a*) Absence versus (*b*) presence in botryoids or thyrsoids of one or more empty bracts (metaxyphylls; terminology of Briggs and Johnson 1979) below the terminal flower (fig. 1.6).
7. Presence of metatopies: position of subtending floral bracts either (*a*) below or (*b*) above the branching point (fig. 1.7).
8. (*a*) Absence versus (*b*) presence of more than one flower in the axil of a bract: accessory flowers (fig. 1.8).
9. Absence versus presence of ramiflory or cauliflory.
10. Floral bracts (pherophylls and prophylls) more or less persistent up to anthesis versus early caducous.
11. Absence versus presence of long "stalks" in inflorescences; that is, the hypopodium is longer than each following internode in the main inflorescence axis.

An inflorescence may be defined as the reproductive system that is produced in a flush (Weberling 1989). However, in tropical woody plants this definition is often unpractical to apply, especially when flower-bearing branches are interspersed with flowerless branches. Thus, for our purposes we circumscribe inflorescences as the branching systems in which all axes bear flowers. Not only is this easier to achieve (especially also with herbarium material) but also the patterns are more uniform and better comparable at the systematic mesolevel here focused on. These inflorescences are mostly lateral, but they may also be terminal (especially in Calycanthaceae).

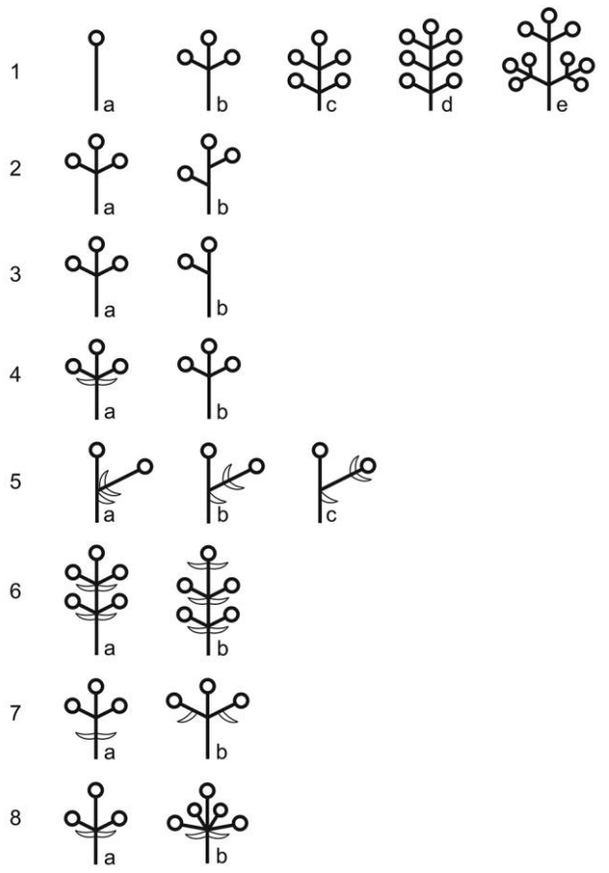


**Fig. 1** Inflorescences of Laurales: ramification patterns of lateral branches of inflorescence main axis and characteristics of bracts (pherophylls and prophylls). (1) Main ramification patterns. a = single flower; b = triad; c = botryoid with five flowers; d = botryoid with seven flowers; e = thyrsoid. Bracts not drawn. (2) Position of the two lateral flowers in a triad. a = opposite; b = alternate. Bracts not drawn. (3) Presence of lateral flowers. a = both lateral flowers present; b = only one lateral flower present. Bracts not drawn. (4) Presence or absence of pherophylls of lateral flowers. a = present; b = absent. Prophylls not drawn. (5) Position of prophylls of lateral flowers on floral axis. a = basal; b = at mid level; c = distal. (6) Metaxyphylls in botryoids. a = absent; b = present. Prophylls not drawn. (7) Metatopies in lateral flowers. a = concaulescent; b = recaulescent. Prophylls not drawn. (8) Presence or absence of accessory flowers. a = absent; b = present. Prophylls not drawn.

## Material and Methods

The information used is based on studies of living or liquid-fixed inflorescences and of herbarium material. Illustrations in publications were also used. In this chapter pickled material and herbarium material studied are listed. For each specimen the collector and collection number are mentioned. If there is no collection number, the year is indicated after "s.n." Herbarium acronyms are indicated at the end of each collection. To further distinguish the collections from cited literature in the text, the initials of the first names are indicated.

### *Atherospermataceae*

*Daphnandra apatela* Schodde; R. Schodde 5123, G.
*Daphnandra dielsii* Perkins; R. Schodde 3258, G.
*Daphnandra micrantha* (Tul.) Benth.; P. Endress 4327, fixed in 70% ethanol, Z; R. Schodde 5146, G.
*Daphnandra repandula* (F. Muell.) F. Muell.; P. Endress 4222, fixed in 70% ethanol; D. Lorence 7190, PTBG, Z; R. Schodde 3254, G.
*Doryphora aromatica* (F.M. Bailey) L.S. Sm.; D. Lorence et al. 7181, PTBG.
*Laurelia sempervirens* Tul.; O.Buchtien s.n., 25 Nov. 1898, Z.
*Nemuaron vieillardii* (Baill.) Baill.; H. MacKee 13429, Z.

### *Calycanthaceae*

*Calycanthus chinensis* (W.C. Cheng & S.Y. Chang) P.T. Li; P. Endress 98-123, fixed in 70% ethanol, Z.
*Calycanthus floridus* L.; P. Endress 3803a, fixed in FAA, Z.
*Calycanthus occidentalis* Hook. & Arn.; P. Endress 7478a, fixed in ethanol, Z.
*Chimonanthus nitens* Oliv.; P. Endress 03-113, fixed in ethanol, Z.
*Chimonanthus praecox* (L.) Link; P. Endress 2257, fixed in FAA, Z.
*Idiospermum australiense* (Diels) S.T. Blake; P. Endress 4223, fixed in FAA, Z; T. Flinn 7186, PTBG, Z.

### *Gomortegaceae*

*Gomortega keule* (Molina) Baill.; T. Stuessy, D. Crawford, P. Pacheco & A. Landero 6698, fixed in 70% ethanol; Bernardi 20683, Z.

### *Hernandiaceae*

*Gyrocarpus americanus* Jacq.; P. Endress 1048a, fixed in FAA, Z.
*Hernandia nymphaeifolia* (Presl) Kubitzki; National Tropical Botanical Garden, Kauai, Hawaii, accession number 920389, voucher: T. Flynn 5612; and P. Endress s.n., 2004, fixed in 70% ethanol, from the same individual, Z.

### *Lauraceae*

*Aiouea acarodomatifera* Kosterm.; R. Klein 1659, Z.
*Aiouea saligna* Meisn.; G. Prance & N. Silva 58606, Z.
*Alseodaphne elongata* (Blume) Kosterm.; W. de Wilde & B. de Wilde-Duyfjes 13919, Z.
*Aniba panurensis* (Meisn.) Mez; J. Ramos 1857, G.
*Beilschmiedia diversiflora* Pierre ex Robyns & R. Wilczek; M. Le Testu 8099, Z.
*Beilschmiedia insularum* Robyns & R. Wilczek; M. Le Testu 7246, Z.
*Beilschmiedia mannii* (Meisn.) Benth. & Hook.f. ex B.D. Jacks.; W. De Wilde 304, Z.
*Beilschmiedia minutiflora* (Meisn.) Benth. & Hook.f. ex B.D. Jacks.; G. Zenker 1695, Z.
*Beilschmiedia recurva* B. Hyland; P. Forster 28167, Z.
*Beilschmiedia tawa* (A. Cunn.) Kirk; H. Travers s.n., s.d., Z; D. Petrie s.n., s.d., Z.
*Cinnamomum burmanni* (Nees & T. Nees) Blume; P. Endress 03-68, fixed in 70% ethanol, Z.
*Cinnamomum camphora* (L.) J. Presl; P. Endress 2605, fixed in FAA, Z.
*Cinnamomum verum* J. Presl; F. Fosberg 60444, PTBG.
*Cryptocarya alba* (Molina) Looser; G. Geisse s.n., 1912, Z.
*Cryptocarya aschersoniana* Mez; G. Hatschbach 55766, Z.
*Cryptocarya gracilis* Schltr.; G. McPherson 6244, PTBG.
*Cryptocarya impressa* Miq.; Griffith s.n., 1863–4, ZT; East India Company 4277, ZT.
*Cryptocarya lauriflora* (Blanco) Merr.; C. Wenzel 2861, Z.
*Cryptocarya microneura* Meisn.; J. Canfield s.n., 1897, Z.
*Cryptocarya myrtifolia* Stapf; C. Schröter s.n., 30 X 1926, ZT.
*Cryptocarya odorata* Guillaumin; G. McPherson 4283 and 5176, PTBG; M. Balansa 1848, G.
*Endiandra baillonii* (Pancher & Sebert) Guillaumin; G. McPherson 5176, PTBG.
*Endiandra bessaphila* B. Hyland; P. Forster 28166, Z.
*Endiandra cowleyana* F.M. Bailey; P. Forster 28151, Z.
*Endiandra hypotephra* F. Muell.; S. Kajewski 1443, Z.
*Eusideroxylon zwageri* Teijsm. & Binn.; O. Beccari 2611, G.
*Hypodaphnis zenkeri* (Engl.) Stapf; A. Staudt 961, G; Zenker 3033a, Z.
*Nectandra cuspidata* Nees & Mart.; G. Hatschbach 58604, Z.
*Nectandra membranacea* (Sw.) Griseb.; C. Cid Ferreira et al. 10536, PTBG; P. Sintenis 4656, Z.
*Nectandra oppositifolia* Nees & Mart.; Y. Mexia 4461, Z.
*Ocotea aciphylla* (Nees & Mart.) Mez; G. Hatschbach 54799, Z.
*Ocotea amazonica* (Meisn.) Mez; B.M. Boom & A.L. Weitzman 5251, Z.
*Ocotea bicolor* Vattimo-Gil; G. Hatschbach 48235, 50096, Z.
*Ocotea botrantha* Rohwer; P. Endress 1118, fixed in FAA, Z.
*Ocotea bullata* (Burch.) E. Meyer in Drege; Forest Officer, Transkai CC 886, Z.
*Potameia micrantha* van der Werff; H. van der Werff 12777, 12797, both G.
*Potameia thouarsii* Roem. & Schult.; S. Totzafy Be STB 548, G.

### *Monimiaceae*

*Austromatthaea elegans* L.B. Sm.; P. Endress 4196, 4204, both fixed in FAA, Z.
*Decarydendron belenae* Danguy; H. Humbert 6613, G.
*Decarydendron lamii* Cavaco; S. Malcomber et al. 2903, PTBG.
*Ephippiandra madagascariensis* (Danguy) Lorence; G. McPherson 14519, PTBG; L. Gautier & T. Rakotomamonjy LG 3711, PTBG.
*Hedycarya cupulata* Baill.; G. McPherson 4478, 6341, 6344, all PTBG.
*Hedycarya dorstenioides* A. Gray; S. Perlman et al. 16096A, PTBG.
*Hedycarya symplocoides* S. Moore; G. McPherson 3148, PTBG.
*Hortonia angustifolia* Trim.; E. Frey & S. Keppetipola s.n., 1978 = P. Endress 4483, fixed in FAA, Z.
*Levieria forbesii* Perkins; T. Hartley 12700, G.
*Levieria nitens* Perkins; J. Clemens 4561, Z.
*Levieria* sp.; W. Takeuchi 4505, PTBG.

*Macropeplus ligustrinus* (Tul.) Perkins; R. Harley et al. 25108, PTBG.

*Mollinedia minutiflora* Standl. & L.O. Williams; T. Croat & G. Zhu 76649, PTBG; G. McPherson 9888, PTBG.

*Mollinedia viridiflora* Tul.; Ibarra Manriquez 522, PTBG; W.D. Stevens 16960, Z.

*Monimia ovalifolia* Thouars; female, D. Lorence & A. Rolland 2755, 2756, 2757, all Z; male, D. Lorence 2896, Z; D. Lorence 6937, PTBG.

*Monimia rotundifolia* Thouars; male, D. Lorence 2775, Z.

*Palmeria gracilis* Perkins; P. Endress 4060, 4085, 4091, all fixed in FAA, Z.

*Palmeria womersleyi* Philipson; R. Hoogland & R. Schodde 6787, Z.

*Peumus boldus* Molina; P. Endress 4748, pickled, Z; E. Werdermann 311, Z.

*Steganthera ilicifolia* A.C. Sm.; P. Endress 4074, 4126, both fixed in FAA, Z.

*Steganthera laxiflora* (Benth.) Whiffin & Foreman; D. Lorence 7183, PTBG; B. Hyland 9189, Z.

*Steganthera macooraia* (F.M. Bailey) P.K. Endress; P. Endress 4281, 4295, both fixed in FAA, Z.

*Tambourissa hildebrandtii* Perkins; B. Randriamampionona 516, PTBG.

*Tambourissa nosybensis* Lorence; C. Birkinshaw 36, PTBG.

*Tambourissa purpurea* (Tul.) A. DC.; W. Rauh M 138, and cutting cultivated and flowers fixed in FAA, Z.

*Tambourissa trichophylla* Baker; L. Dorr et al. 4384, PTBG.

*Wilkiea austroqueenslandica* Domin; P. Endress 4311, fixed in FAA, Z; J. Tracey 152, Z.

*Wilkiea huegeliana* (Tul.) A. DC.; P. Endress 4331, fixed in FAA, Z.

*Wilkiea macrophylla* A. Cunn.) A. DC.; P. Endress 22.12.78, fixed in FAA, Z.

*Xymalos monospora* (Harv.) Baill.; R. Gereau & C. Kayombo 4149, PTBG; E. Moll 973, Z; A Saxer 45, Z.

### *Siparunaceae*

*Siparuna echinata* (Kunth) A. DC.; J. Feil 01331, Z.

*Siparuna guajalitensis* S.S. Renner & Hausner; J. Feil 01338, Z.

*Siparuna salvioides* Perkins; J. Jaramillo & V. Zak 7870, PTBG.

*Siparuna tetraceroides* Perkins; L. Gomez et al. 20983, PTBG.

*Siparuna thecaphora* (Poepp. & Endl.) A. DC.; P. Endress, fixed in FAA, Z; J. Feil 01331, Z; R. Liesner 26576, PTBG.

## Glossary

Inflorescence terminology follows Weberling (1989) and Endress (2010; but see the last paragraph of the introduction for an exception).

### *Ramification Pattern*

racemose ramification. Flower number unrestricted, but axis orders restricted to two.

cymose ramification. Axis order number unrestricted, but lateral flower number per axis order restricted to one (monochasium) or two (dichasium).

### *Inflorescences*

raceme. Inflorescence with racemose ramification and without a terminal flower.

botryoid. Same but with a terminal flower.

thyrse. Inflorescence with a racemose main axis and cymose lateral axes; main axis without a terminal flower.

thyrsoid. Same but with a terminal flower.

panicle. Inflorescence without restriction of axis orders or of flower numbers per axis; terminal flowers present.

uniflorous inflorescence. Inflorescence consisting of a single flower.

triad. A unit of a terminal flower and two lateral flowers. As such, it could be a poor cyme (dichasium) or a poor botryoid. We named it one way or the other depending on whether the same individual showed richer units in the form of cymes or botryoids.

### *Other Terms*

hypopodium. The part of an axis below its first node.

metatopy. The congenital fusion of a pherophyll with the lateral axis it bears or the fusion of a lateral axis with the main axis so that the pherophyll seems displaced backward on the main axis (Weberling 1989).

metaxyphyll. (An) empty bract(s) below the terminal flower of a botryoid, thyrsoid, or panicle.

pherophyll. A leaf or bract that bears a lateral shoot or flower.

prophylls. The first two leaves or bracts of a lateral shoot or pedicel.

## Results (Including a Review of Published Illustrations)

### *Calycanthaceae*

The monotypic genus *Idiospermum* is sister to all other extant Calycanthaceae (Qiu et al. 1999; Doyle and Endress 2000; Hilu et al. 2003), which have been referred to as Calycanthoideae. *Sinocalycanthus* appears to be nested in *Calycanthus* (Zhou et al. 2006). Calycanthaceae are characterized by large flowers that occur singly or in simple ramification systems of few flowers.

**Calycanthaceae–Idiospermoideae–Idiospermum.** The flowers of the only species, *Idiospermum australiense*, are bisexual (among them a few male ones were also found; see also Staedler et al. 2007); they are single (P. Endress et al. 4223), in triads (P. Forster 25936), or in few-flowered botryoids (T. Flynn 7186, PTBG). The floral axes (lateral and main axes; if the main axis is branched, both the basal and distal parts) carry several pairs of bracts, which fall off sometime before anthesis.

1. Thus, branching is zero or of the first order.
2. Branching is opposite.
3. Branching is symmetric.
4. Prophylls are present.
5. Prophylls are relatively basal.
6. Metaxyphylls are present.
7. Metatopies are absent.
8. Accessory buds?
9. Ramiflory and cauliflory appear to be absent.

10. Bracts are caducous.
11. A long stalk is absent.

**Calycanthaceae–Calycanthoideae.** Flowers are bisexual; they are commonly single in all genera. In *Calycanthus occidentalis*, triads (a terminal and two lateral flowers) may also be present (Parkin 1914; Weberling 1988); we also found dichasia with higher orders: heptads or one of the branches (exceptionally) with an additional branching order. The highly branched forms may be described as thyrsoids with two dichasia. In both *Chimonanthus* and *Calycanthus* the floral axis begins with bract-like organs; they need a longer "takeoff" to produce more typical tepals.

1. Thus, branching is zero, of the first order, or of the first and second or (exceptionally) third order. However, it is not certain whether the highest-order flowers develop up to anthesis, as they appear much delayed. This is most pronounced in *Chimonanthus praecox*.
2. Branching is (more or less) opposite.
3. Branching is symmetric.
4. Prophylls are present.
5. Prophylls are basal, as additional bracts are intercalated between prophylls and tepals (however, without long internodes between them).
6. Metaxyphylls are present.
7. Metatopies are absent.
8. *Calycanthus floridus* (Baillon 1869; Weberling 1988) and *C. praecox* (Weberling 1988) have an abaxial accessory bud in the axil of the leaf that bears the inflorescence. In *C. floridus*, this accessory bud may later terminate in a flower (Baillon 1869). Such an accessory bud was also found in *Calycanthus chinensis*, *C. occidentalis*, and *Chimonanthus nitens*.
9. Ramiflory and cauliflory are absent.
10. Bracts are caducous in some species.
11. A long stalk is absent.

### *Gomortegaceae*

Flowers of the single species of the family, *Gomortega keule*, are bisexual; they are in simple botryoids; the lateral flowers are in pairs and opposite (decussate) in the axil of small bracts. Botryoids contain 3–9 flowers, mostly 7 (L. Bernardi 20683; T. Stuessy et al. 6698), and up to 11 (illustration in Rodríguez et al. 1983). A drawing in Ruíz and Pavón (1798–1802) shows three inflorescences with the first pair of flowers replaced by triads (thus, a thyrsoid), followed by two pairs of single flowers.

1. Branching is commonly of the first order but goes up to the second order.
2. Branching is opposite.
3. Branching is symmetric.
4. Prophylls are present in the outermost branches.
5. Prophylls are distal.
6. Metaxyphylls are present.
7. Metatopies are lacking.
8. Accessory flowers are lacking.
9. Ramiflory and cauliflory have not been reported.
10. Floral bracts are early caducous.
11. The stalk of the inflorescence or of partial inflorescences is not longer than the following internodes.

### *Atherospermataceae*

*Daphnandra* and *Doryphora* form a clade that is sister to the remainder of the family with weak support (Renner et al. 2000). Among this remainder, *Dryadodaphne* is sister to the rest, and *Atherosperma* plus *Nemuaron* is sister to *Laurelia*; *Laureliopsis* is nested in *Laurelia* (Renner et al. 2000).

Flowers are bisexual in *Daphnandra*, *Doryphora*, *Dryadodaphne*, and *Nemuaron* but unisexual in *Laurelia* (Renner et al. 2000). Flowers are single (*Atherosperma*) or, most commonly, in botryoids. *Doryphora sassafras* (P. Endress 2256) and *Doryphora aromatica* (Schodde 1969) have botryoids with three flowers; *D. aromatica* may also have compound (double) botryoids (D. Lorence et al. 7181). *Dryadodaphne* (Schodde 1969) and *Nemuaron* have botryoids with three or five flowers (Schodde 1969; Jérémie 1982*a*; P. K. Endress, personal observations). In *Laurelia sempervirens* and *Laurelia novae-zelandiae* botryoids with seven to nine flowers are present. In the latter, instead of the two lowermost lateral flowers, two botryoids of five flowers may also be present, thus forming a compound botryoid (Sampson 1969). In *Daphnandra repandula* (P. Endress 4222) there are triads at the base of the inflorescence; thus, they may be viewed as compound botryoids or thyrsoids (D. Lorence 7190). Compound botryoids are present in *Daphnandra micrantha* (R. Schodde 5146). Compound botryoids (diplobotryoids) in *Daphnandra* are also figured by Schodde (1969) and compound thyrses by Tulasne (1855). Male and female flowers may occur in the same inflorescence. In *L. novae-zelandiae* A. Cunn., the terminal flower of a botryoid is almost always male in mixed inflorescences; otherwise, no special pattern was found (Sampson 1969).

1. Branching goes up to the second order (*Daphnandra*, *Laurelia*; Schodde 1969), in *D. micrantha* exceptionally up to the fourth order (Tulasne 1855).
2. Branching is opposite or almost so (Schodde 1969): 1 alternate, 2 opposite in *D. repandula* (D. Lorence 7190) or 1, 2 opposite in *D. aromatica* (D. Lorence et al. 7181), *L. novae-zelandiae* (Sampson 1969), *Nemuaron vieillardii* (H. MacKee 13429), *Daphnandra apatela* (R. Schodde 5123); 1 almost opposite, 2 opposite in *D. micrantha* (R. Schodde 5146); 1 opposite (only degree 1 present) in *L. sempervirens* (O. Buchtien s.n., 25 Nov. 1898) and *N. vieillardii* (H. MacKee 13429; M. Baumann-Bodenheim 15129).
3. Branching is commonly symmetric (Schodde 1969).
4. Prophylls in the branches of the highest order are present in *Dryadodaphne* and *Laureliopsis* (Schodde 1969), infrequently in *L. novae-zelandiae* (Sampson 1969).
5. Position of prophylls, if branches are extended, is distal (i.e., immediately below the flowers they precede; Schodde 1969).
6. A pair of empty bracts (metaxyphylls) is present in *Doryphora* (Schodde 1969; D. Lorence 7181) and *Nemuaron* (H. MacKee 13429) and is present or absent in *L. novae-zelandiae* (Sampson 1969).
7. Metatopies appear to be absent (Schodde 1969; P. K. Endress, personal observations).
8. Accessory flowers are present in the inflorescences of *Daphnandra* and *D. sassafras* (Weberling 1988). In *D. aromatica* in a compound botryoid there are accessory buds abaxially in the bracts that bear botryoids. In *D. apatela* accessory flowers were found in the adaxial and abaxial position at the same

branching point (R. Schodde 5123). In *D. repandula* accessory flowers are on the abaxial side (R. Schodde 3254; P. Endress 4222; illustration in Perkins 1925). In *D. micrantha* they are on the adaxial side (Tulasne 1855; Schodde 1969; R. Schodde 5146); an accessory bud may be present on the adaxial side of the base of the inflorescence (not certain whether vegetative or floral; P. Endress 4327). In *Daphnandra dielsii* accessory botryoids were found adaxially in an inflorescence (R. Schodde 3258). In *Nemuaron*, accessory flowers were not found.

9. Ramiflory and cauliflory appear to be absent (Schodde 1969).

10. Floral bracts are often persistent (Schodde 1969; P. K. Endress, personal observations). In *L. novae-zelandiae* the lowermost bracts in an inflorescence are persistent; the others abscise before anthesis (Sampson 1969).

11. Long stalks are absent.

### *Siparunaceae*

The small African genus *Glossocalyx* is sister to the larger American genus *Siparuna*, and *Bracteanthus* is nested in *Siparuna* (Renner and Won 2001; Renner and Hausner 2005). Flowers are unisexual, and dioecy evolved several times from monoecy (Renner and Won 2001). In monoecious species female flowers are predominantly in the more basal area of the inflorescences and male flowers in the distal area (Renner and Hausner 2005). Siparunaceae are characterized by extensive, sometimes multiflowered dichasial-monochasial (basally dichasial) systems (most pronounced in *Siparuna*). Such monochasia may have the superficial appearance of racemes. However, the one-sidedness and the position of bracts may indicate their nature as monochasia (e.g., fig. 5*D* in Renner and Hausner 2005). If inflorescences are mixed, female flowers tend to be in the first branches of the cymes and male flowers in the later branches (Renner and Hausner 2005). These monochasia occur singly or in groups. Usually, there are two lateral cymes in the axil of a foliage leaf, with the main branch consisting of a (vegetative?) bud. This was seen in herbarium specimens of a number of species. This feature was illustrated for *Siparuna apiosyce* (Tulasne 1855, 1857; Weberling 1988) and *S. mollis* (Tulasne 1855). Such a system may be viewed as a thyrse. However, the structure in Siparunaceae is quite different from thyrses (thyrsoids) that occur in Monimiaceae or other Laurales. Another pattern of the cymes is repeated dichasial branching before the onset of monochasial branching (e.g., several times in *S. multiflora*: Renner and Hausner 1996; twice in *S. thecaphora* [R. Liesner 26576], three to four times in *S. echinata* [J. Feil 91331], and *S. guajalitensis* [J. Feil 91348]). An example with especially many-flowered monochasia is *S. reginae*, whose cymes have 30–80 flowers (Renner and Hausner 1997). Such extensively branching monochasia have flowers at very different stages of development. In thyrses with several lateral branches with dichasial-monochasial cymes, the dichasial parts without a terminal flower may also occur, such as in *S. salvioides* (J. Jaramillo & V. Zak 7870).

1. Branching orders few up to 40 (because of extensive monochasial branching; *S. reginae*; Renner and Hausner 1997).

2. Branching: 1 opposite, 2 almost opposite, 3 and following monochasial in *S. mollis* (Tulasne 1855).

3. Branching is symmetric in the dichasial part but, of course, asymmetric in the monochasial part.

4. Presence or absence of prophylls (and floral bracts in general) is difficult to establish from herbarium material because of the often dense pubescence.

5. Position of prophylls unknown

6. Not applicable because inflorescences are not botryoids.

7. In *S. tetraceroides* or *S. macra* (L. Gómez et al. 20983), which has lax inflorescences, the subtending bract of each of the two monochasia of the thyrse is fused with the pedicel of the flower of the first order (bracts of the upper branches are not visible).

8. In *Glossocalyx* single flowers are common or sometimes two (Perkins and Gilg 1901, fig. 28; Perkins 1925, fig. 47). It is not clear whether the second smaller (inner, adaxial) flower is an accessory flower or part of a poorly developed monochasium (Perkins and Gilg 1901, fig. 28). It could also be that they are produced from separate buds in a ramiflorous system (in older shoots; see 9).

9. Ramiflory (and cauliflory) is common in *Glossocalyx* and *Siparuna*.

10. Floral bracts in *Siparuna* are mostly small and early caducous (Renner and Hausner 2005).

11. Long stalks are not present. The main axis of the inflorescence is often extremely short (almost zero).

### *Monimiaceae*

Monimiaceae consist of two major clades: Monimioideae (*Monimia*, *Palmeria*, *Peumus*) and Mollinedioideae (all other genera; Renner 1998, 2002). *Hortonia* is sister to all other Mollinedioideae (Renner 1998, 2002), which form a grade with the Malagasy *Decarydendron* and *Tambourissa*, followed by the western Pacific *Hedycarya*, *Levieria*, and *Kibaropsis*, followed by the African *Xymalos* and the unresolved remainder of the subfamily (Renner 2002). *Hortonia* was also earlier considered to be "basal" in the family, as its floral structure is less specialized than that of other Mollinedioideae (Endress 1980*a*, 1980*b*) and it is the only Monimiaceae with bisexual flowers. Therefore, *Hortonia* is here presented separately. Inflorescences in Monimiaceae are relatively diverse, as it is a genus-rich family. However, there are some idiosyncratic tendencies in the family. We consider Monimioideae, Mollinedioideae, and *Hortonia* of Mollinedioideae separately.

**Monimiaceae–Monimioideae.** Common forms in Monimioideae inflorescences are botryoids or mixed forms representing botryoids/thyrsoids with triads instead of single lateral flowers, either in all branches (apart from the uppermost pair, which then forms a triad with the terminal flower) or only in the basal branches (*Monimia*: Perkins 1925; Lorence 1985; *Peumus*: Pax 1889*b*; Peixoto et al. 2001; some *Palmeria*: Perkins 1925; Philipson 1986). In *Palmeria* (*Palmeria womersleyi*) compound botryoids/thyrsoids may also occur (Philipson 1986); this is also the case in *Palmeria gracilis* (P. Endress 4091) and *Palmeria arfakiana* (as *Palmeria warburgii*; Perkins 1925). The same is true for *Monimia ovalifolia* (female: D. Lorence & A. Rolland 2757; male: D. Lorence 2896) and *Monimia rotundifolia* (Perkins 1925). Compound botryoids occur in *M. ovalifolia*, with

three to five flowers in lateral botryoids (D. Lorence 2896, 6937), and *P. gracilis*, with two to nine flowers in lateral botryoids (P. Endress 4091).

*Palmeria* is diverse in the branching orders. *Palmeria scandens* has simple botryoids with seven flowers (Stanley and Ross 1983), whereas *P. arfakiana* (as *P. warburgii*), which has compound thyrsoids, shows branching of up to the third order (Perkins 1925).

1. Branching: two orders in *Palmeria clemensae* and *P. womersleyi* (Philipson 1982), one to three orders in *P. gracilis* (P. Endress 4085, 4091), three orders in *P. arfakiana* (as *P. warburgii*; Perkins 1925).

2. Branching: 1 opposite, *Peumus boldus* (E. Werdermann 311); 1 more or less opposite, *P. gracilis* (P. Endress 4085); 1 subopposite, 2 alternate or opposite, 3 opposite: *P. gracilis* (P. Endress 4091); 1, 2 opposite: *M. ovalifolia* (D. Lorence 2896, 6937), but also 1, 2 alternate in the same species (D. Lorence & A. Rolland 2756); 1, 2, 3 opposite: *M. rotundifolia*, male (D. Lorence 2775).

3. Branching is symmetric.

4. Prophylls seem to be lacking in the outermost branches in *Palmeria*.

5. Not applicable for *Palmeria*.

6. In *P. boldus* (P. Endress 4748) the uppermost pair of bracts in an inflorescence is empty (metaxyphylls); this is sometimes also the case in *P. gracilis* (P. Endress 4060). In *Monimia* metaxyphylls were not found.

7. Metatopies: In *P. gracilis* (P. Endress 4060, 4085) the lower flowers or also the upper flowers in a botryoid may have their subtending bracts on the pedicel; in *P. gracilis* (P. Endress 4091) and in *P. womersleyi* (R. Hoogland & R. Schodde 6787) this was seen only in the distal part of the inflorescence. This was also observed in *M. ovalifolia* (D. Lorence 2896). The reverse may be present in *Monimia* (observed in *M. ovalifolia*), where the subtending bracts of the lateral flowers appear to be below the branching point, but this needs closer study. The subtending bracts of the uppermost pair of flowers (on the pedicels) may be very small (reduced), or, conversely, the uppermost pair of bracts may be empty (metaxyphylls).

8. Accessory flowers were not found.

9. Cauliflory is not known in Monimiaceae–Monimioideae. For some species of *Monimia* ramiflory is reported (Lorence 1985).

10. Floral bracts of the first order are partly still present at anthesis, whereas the others have fallen, such as in *P. gracilis* (P. Endress 4091), *M. ovalifolia* (D. Lorence & A. Rolland 2755), and *M. rotundifolia* (D. Lorence 2775). Most bracts have fallen in *M. ovalifolia* (D. Lorence & A. Rolland 2757).

11. A long stalk may be present in *Palmeria* but not in *Monimia* and *Peumus*.

**Monimiaceae–Mollinedioideae–*Hortonia*.** In *Hortonia*, the genus that appears basal in Mollinedioideae (Renner 1998, 2002), the inflorescences of *Hortonia angustifolia* are botryoids or thyrsoids (with triads as cymose modules); accessory (external, abaxial) flowers and accessory (external, abaxial) inflorescences were observed (this study). Baillon (1869) depicts *Hortonia floribunda* with thyrsoids (with triads as cymose modules). Wight (1853) illustrates *H. floribunda* with botryoids (and one thyrsoid with a triad?), some of the floral subtending bracts with an accessory flower (internal?), and some inflorescences with an accessory branch at the base (external, abaxial).

1. The number of branching goes up to the second order.

2. Branching is opposite.

3. Branching is symmetric.

4. The outermost branches do have organs in prophyll position (transverse). However, they are more or less integrated in the floral architecture.

5. They are distal.

6. Metaxyphylls are present.

7. Metatopies are lacking.

8. Accessory branches occur on both sides of the inflorescence branches, at the base of the inflorescence in an abaxial position, but higher up in an adaxial position in *H. angustifolia* (G. Thwaites 1026) or only in an abaxial position (P. Endress 4483, Z).

9. Ramiflory and cauliflory appear to be lacking.

10. Floral bracts are more or less persistent.

11. Stalks are relatively long (Wight 1853).

**Monimiaceae–Mollinedioideae without *Hortonia*.** Among Mollinedioideae, flowers are single, in triads, or in botryoids of five or more flowers. Sometimes, instead of single lateral flowers in a botryoid, lateral triads or botryoids are present. Thus, the inflorescences may be described as simple or compound botryoids or as thyrsoids. All these forms may occur in a genus, such as in *Tambourissa* (Lorence 1985). It is not known to us whether there are thyrsoids with cymes that are larger than triads.

Solitary flowers occur, for example, in *Decarydendron ranomafinensis* (Lorence and Razafimandimbison 2002), *Ephippiandra microphylla* (Cavaco 1959), *Ephippiandra myrtoidea* (Perkins 1898), *Hedycarya parvifolia* (Jérémie 1982*b*), *Macropeplus* (da Silva Santos and Peixoto 2001), *Steganthera macooraia* (Endress 1979), *Tambourissa monongarivensis* (Lorence 2002), and together with inflorescences in a number of other *Tambourissa* species (Lorence 1985). Single flowers in groups (cauliflorous) are present in *Kibaropsis* (Jérémie 1982*b*).

Botryoids of three flowers (triads) are common in *Macropeplus* (Tulasne 1855, 1857; da Silva Santos and Peixoto 2001) and in *Mollinedia* (e.g., Tulasne 1855, 1857; Peixoto 1979; Renner and Hausner 1997; Lorence 1999*b*; Peixoto et al. 2001). More rare are botryoids that occur with five or more flowers in *Mollinedia* (Peixoto 1987). Botryoids with three flowers were also found in *Steganthera ilicifolia* (P. Endress 4074). Botryoids with three or more flowers are sometimes present in *Ephippiandra* (Lorence 1999*a*).

Botryoids with five or more flowers are especially common. They occur, for example, in *Kairoa*, *Matthaea*, and *Lauterbachia* (Philipson 1986); *Ephippiandra* (Cavaco 1959); *Tambourissa* (Jérémie and Lorence 1991); *Hennecartia* (Perkins 1925); and *Decarycendron helenae* (H. Humbert 6613). Botryoids with three, five, seven, or nine flowers, or single-flowered inflorescences, occur in *Hedycarya* (Jérémie 1978, 1982*b*, 1983) and *Tambourissa* (Tulasne 1855; Cavaco 1959; Jérémie and Lorence 1991; P. K. Endress, personal observations). Up to 9 or 11 flowers are present in *Wilkiea huegeliana* (P. Endress 4331). In *Hedycarya* compound botryoids were also observed (*Hedycarya dorstenioides*; Jérémie 1978). Botryoids with three or five

flowers occur in *Levieria* (Philipson 1986). Compound botryoids are present in some *Steganthera* (Perkins 1911, 1925) and in *Hedycarya arborea* (Cheeseman 1914). Botryoids terminating in a vegetative bud instead of a flower are present in *Mollinedia viridiflora* (Ibara M. 522).

Thyrsoids with triads instead of single lateral flowers in a botryoid occur in *Hedycarya loxocarya* (Jérémie 1983), *Levieria urophylla* (Perkins 1911), *Levieria forbesii* (T. Hartley 12700), *Kibara serrulata* (Perkins 1925), *W. huegeliana* (P. Endress 4331), some *Steganthera* (Perkins 1925; Kanehira and Hatusima 1942; Philipson 1986), some *Mollinedia* (Perkins 1900), and some *Tambourissa* (Lorence 1985). Dyads instead of triads were also found in *Kibara* (Philipson 1985), *W. huegeliana* (P. Endress 4331), and *Tambourissa* (Jérémie and Lorence 1991). Compound thyrsoids were seen in *Steganthera laxiflora* (Benth.) Whiffin & Foreman (D. Lorence 7183).

A rare and odd feature are single flowers that are preceded by a large number of empty bracts (*Hedycarya perbracteolata*: Jérémie 1983; *Tambourissa cocottensis*: Lorence 1985).

In some genera the inflorescence tends to end in a (vegetative?) bud, not a flower, such as in *Macropeplus* and *Mollinedia*. In such cases it is not always certain whether the single triads make up inflorescences or whether the entire thyrse of all the triads together has been formed as a unit.

Male and female flowers may occur in the same inflorescence. In *Tambourissa purpurea* lateral flowers of a botryoid are always male; the terminal flower is either female or male (W. Rauh M 138). In other cases inflorescences are not mixed or species are dioecious; for example, in *Tambourissa* there are monoecious and dioecious species, and in monoecious species there are some with uniform and others with mixed inflorescences (Lorence 1985).

1. In general, branching does not reach high orders, usually not more than the third order (e.g., up to the third order in *Hedycarya*; see figures in Jérémie 1978; in *Levieria* see figures in Philipson 1980; in *Steganthera* see Philipson 1984, 1986).

2. Branching in botryoids is mostly opposite; however, it may be more or less alternate in *Decarydendron* (Cavaco 1959) or opposite or alternate in *Wilkiea austroqueenslandica* (J. Tracey 152; P. Endress 4311). It is opposite in *Mollinedia minutiflora* (T. Croat & G. Zhu 76649; G. McPherson 9888), *M. viridiflora* (Ibarra M. 522), *Macropeplus ligustrinus* (R. Harley et al. 25108), *Ephippiandra madagascariensis* (G. McPherson 14519; and other specimens), *Hedycarya cupulata* (G. McPherson 4478, 6341, 6344), *Hedycarya symplocoides* (G. McPherson 3148), *H. dorstenioides* (S. Perlman et al. 16096A), *Tambourissa hildebrandtii* (B. Randriamampionona 516), and *Xymalos monospora* (R. Gereau & C. Kayombo 4149). In thyrsoids and compound thyrsoids it is also commonly opposite: 1, 2 opposite: *Levieria* sp. (W. Takeuchi 4505); 1, 2, 3 opposite: *Levieria nitens* (J. Clemens 4561). However: 1 alternate, 2 opposite (but distally 1 also opposite) in *Steganthera laxiflora* (D. Lorence 7183).

3. Branching is symmetrical in *S. laxiflora* (D. Lorence 7183) and *L. nitens* (J. Clemens 4561). Whether (rare) asymmetrical ones occur in other species was not recorded here.

4. Floral prophylls in the outermost branches are commonly absent. However, they are present in some flowers of *W. huegeliana* (P. Endress 4331) and in some flowers of *W. austroqueenslandica* (P. Endress 4311). They are present in *Ephippiandra* (Lorence 1985, p. 32) and *M. viridiflora* (G. Ibarra M. 522).

5. Prophylls are close to the base of the pedicel in *W. huegeliana* (P. Endress 4331), near the middle in *L. urophylla* (Perkins 1925), and in the middle or distal in *W. austroqueenslandica* (P. Endress 4311).

6. Often in botryoids the uppermost pair of bracts on the primary axis does not have a flower in their axils (metaxyphylls). This was observed in *H. cupulata* (G. McPherson 6344), *H. symplocoides* (G. McPherson 3148), *L. urophylla* (Perkins 1925), *Levieria squarrosa* (Philipson 1986), *Tambourissa trichophylla* (Cavaco 1959), *T. purpurea* (W. Rauh M 138), *Tambourissa dorri* (Jérémie and Lorence 1991), *T. hildebrandtii* (B. Randriamampionona 516), *T. trichophylla* (L. Dorr et al. 4384), *S. ilicifolia* (P. Endress 4126), and *W. huegeliana* (P. Endress 4331). In *Hedycarya baudouinii* (Perkins 1911, as *Carnegieodoxa*) and *T. purpurea* (W. Rauh M 138) the uppermost pair of empty bracts may be high up on the floral cup of the terminal flower.

7. The floral subtending bracts are not always exactly at the branching point but can be lower or higher (metatopies). A common tendency in botryoids is that the subtending bracts of the distal lateral flowers are above the branching point on the lateral axes; in botryoids with several pairs of flowers the position may then gradually change from the proximal to the distal flower pairs. This was observed in *Decarydendron lamii* (S. Malcomber et al. 2903), *H. cupulata* (G. McPherson 4478, 6341, 6344, PTBG), *H. dorstenioides* (S. Perlman et al. 16096A, PTBG), *Levieria* sp. (W. Takeuchi 4505), *S. ilicifolia* (P. Endress 4126), *Steganthera* cf. *laxiflora* (B. Hyland 9189), and *X. monospora* (E. Moll 973). The same holds for thyrsoids with the subtending bracts of the triads, such as in *S. laxiflora* (D. Lorence 7183), *Austromatthaea elegans* (P. Endress 4196, 4204), *Tambourissa nosybensis* (C. Birkinshaw 36), and *X. monospora* (A. Saxer 45). In *Levieria* sp. (W. Takeuchi 4505) this kind of metatopy was seen in both axes of the first and second order. In *Steganthera stevensii* (Takeuchi 2001), the subtending bracts are large and seem to be fused with the flowers. The opposite kind of metatopy was found in a flower at the base of the botryoid in *W. austroqueenslandica* (P. Endress 4311): its subtending bract was below the attachment of the flower.

8. In some genera accessory flowers were observed. They are abaxial in *E. madagascariensis* (G. McPherson 14519; L. Gautier & T. Rakotomamonjy LG 3711) and *T. nosybensis* (C. Birkinshaw 36), *T. purpurea* (W. Rauh M 138), *Tambourissa leptophylla* (as *Ambora leptophylla*; Tulasne 1855), and *S. laxiflora* (D. Lorence 7183). They are adaxial in *S. ilicifolia* (P. Endress 4074); sometimes even two adaxial accessory flowers were found associated with a flower. They probably also occur in other *Steganthera* species (as indicated by the illustrations in Philipson 1984). Adaxial accessory flowers likely also occur in *Steganthera riparia* (Kanehira and Hatusima 1942). An abaxial accessory inflorescence branch was seen in *S. laxiflora* (D. Lorence 7183). If the illustration in Perkins (1925) is correct, in *M. ligustrinus* adaxial and abaxial accessory branches may be present. Accessory flowers are also mentioned for *Xymalos* (as *Paxiodendron*) by Weberling (1985).

9. A common tendency in Monimiaceae–Mollinedioideae is the presence of ramiflory and cauliflory. In this case, there are either solitary flowers, for example, in *Kibaropsis* (Jérémie 1982*b*), or one or several botryoids, such as in *Hedycarya engleriana* and *Hedycarya chrysophylla* (Jérémie 1982*b*) or

*Ephippiandra* (Lorence 1985) and solitary flowers or inflorescences in *Tambourissa* (Lorence 1985, 2002). Thyrsoids (Perkins 1925) or botryoids (Philipson 1985, 1986) occur in *Kibara* and thyrsoids or compound botryoids in *Steganthera* (including *Anthobembix*; Perkins 1925).

10. The floral bracts are commonly persistent through anthesis.

11. Long stalks are common.

### *Lauraceae*

*Hypodaphnis* tends to appear as sister to all other Lauraceae in Chanderbali et al. (2001), as is the case in the analysis by Renner and Chanderbali (2000), but with fewer taxa studied. This is supported in the more extensive study by Rohwer and Rudolph (2005) and further resolved by Rohwer et al. (2014). The genera *Potoxylon*, *Eusideroxylon*, *Aspidostemon*, *Cryptocarya*, *Beilschmiedia*, *Endiandra*, and *Potameia* (Cryptocaryeae sensu van der Werff and Richter 1996) tend to form a clade that is sister to a large clade containing the bulk of the genera of the family, according to the combined analysis of several sites of the plastid and nuclear genome by Chanderbali et al. (2001; here called "the large clade"). The phylogenetic topology is similar but less well resolved in the *matK* study by Rohwer (2000). The highly modified parasite *Cassytha* had an unstable phylogenetic position in the family, either somewhere in the basal group or in the more derived Lauraceae (Rohwer and Rudolph 2005). However, according to Song et al. (2017), it appears to be the next clade of the grade following Cryptocaryeae and sister to the remainder of the family. Since the cladograms of Lauraceae are highly asymmetrical (Chanderbali et al. 2001), *Hypodaphnis* or *Hypodaphnis* plus Cryptocaryeae may be called "basal" Lauraceae. Cryptocaryeae appear less innovative in floral structure than some groups of the remainder of the family. Thus, it is of interest to consider in what respect Cryptocaryeae and *Hypodaphnis* differ from the remainder of the family in inflorescence structure; we treat them separately. Bisexual flowers are predominant in Lauraceae. However, unisexual flowers occur in several of the highly nested Laureae (e.g., *Actinodaphne*, *Cinnadenia*, *Iteadaphne*, *Laurus*, *Lindera*, *Litsea*, *Neolitsea*; Rohwer 1993*a*). Whether they are unisexual in the basal *Hypodaphnis* as often claimed is insufficiently known (J. Rohwer, personal communication). The size of the inflorescences with respect to flower number in Lauraceae exhibits a great range in many genera (e.g., between two and hundreds in *Ocotea*; Rohwer 1986).

According to earlier authors, inflorescences of Lauraceae are botryoids, thyrses, thyrsoids, paniculate-thyrsoid forms, or racemes; also compound forms of these patterns occur (Weberling 1985, 1988; Rohwer 1986, 1993*a*,1993*b*). We are interested to know whether there are particular forms of these general types that characterize the family or parts of the family.

According to van der Werff and Richter (1996) and van der Werff (2001), genera of the Cryptocaryeae (*Beilschmiedia*, *Cryptocarya*, *Endiandra*, *Potameia*, *Triadodaphne*—the last one included in *Endiandra* by Rohwer 1993*a*) typically have inflorescences with alternate ramifications. They call this inflorescence type "paniculate-more or less cymose" (van der Werff and Richter 1996) and "paniculate" (van der Werff 2001). However, the description is somewhat vague, and the illustration is not clear enough to convey differences from their other inflorescence type, which they call "paniculate-cymose" (van der Werff and Richter 1996) and "paniculate-racemose" (van der Werff 2001) and which is present in the bulk of Lauraceae. Their illustration of this latter type indicates that it is a thyrsoid in the sense of Weberling (1985).

From our observations, botryoids (and compound botryoids) and thyrsoids (and compound thyrsoids) dominate in Lauraceae. Panicles in their ideal form (with continuously richer lateral branching of the inflorescence from top downward), as well as thyrses and racemes, are much more rare. Among the thyrsoids, forms with triads and heptads as cymose units are especially common. Further, these thyrsoids are often characterized not just by the presence of a terminal flower (as opposed to thyrses as defined by Weberling 1989) but also by the presence in the terminal position of the same kind of module that forms the lateral branches. Thus, thyrsoids with lateral triads also tend to be terminated by a triad, and thyrsoids with lateral heptads also tend to be terminated by a heptad (e.g., *Cinnamomum verum*, *Nectandra membranacea*, C. Cid Ferreira et al. 10536, *Persea americana*; Pax 1889*a*). Some thyrses have lateral cymes without a terminal flower, and in these the terminal module also lacks a terminal flower. These may still be referred to as a kind of thyrsoids because they are terminated by a cymose module.

**Lauraceae–*Hypodaphnis*.** The only species of *Hypodaphnis*, *Hypodaphnis zenkeri*, may have unisexual flowers (Rohwer 1993*a*; J. Rohwer, personal communication); the inflorescences are thyrsoids consisting of two dichasia and up to fourth- or fifth-degree branches or compound thyrsoids (G. Zenker 3033a; A. Staudt 961; illustration in Fouilloy 1965). Similar inflorescences are also present in *Nectandra egensis* (cf. Rohwer 1993*b*).

1. Branching: up to the fourth or fifth degree.

2. Branching order 1 is more or less alternate; 2, 3, 4 more or less opposite (order 5 only on one side).

3. Branching is symmetric.

4. It is not known whether prophylls are present or absent.

5. Prophyll position is not known.

6. Not applicable, because flowers are not botryoids.

7. Metatopies are pronounced. The bracts that subtend axes of order 2, 3, 4 are fused with these axes for a long distance, almost up to the branching of axes of the next order (A. Staudt 961, G).

8. Accessory flowers were not found (A. Staudt 961).

9. Ramiflory and cauliflory were not found (A. Staudt 961).

10. Bracts are persistent in the outermost branches (A. Staudt 961).

11. The inflorescence has a long stalk (A. Staudt 961).

**Lauraceae–Cryptocaryeae.** Flowers are bisexual (Rohwer 1993*a*). Some *Endiandra* species appear to have botryoids or compound botryoids (Hyland 1989). *Endiandra sebertii* has botryoids with seven to nine flowers (Kostermans 1974*a*). In *Endiandra poueboensis* the lowermost flower of the botryoid may have a lateral branch (thus, dyad?; Kostermans 1974*a*). Compound botryoids are present in *Beilschmiedia minutiflora* (G. Zenker 1695) and *Beilschmiedia insularum* (M. Le Testu 7246). *Endiandra ochracea* has compound botryoids, each botryoid with three to seven flowers (Arifiani 2001). Richly branched compound botryoids of two to five flowers per

botryoid (or per panicle branch) occur in *Potameia thouarsii* (S. Totzafy Be STB 548), similarly (botryoids of two to six flowers) in *Potameia micrantha* (H. van der Werff et al. 12777). Compound botryoids—each botryoid with numerous minute flowers—seem to be present in *P. micrantha* (H. van der Werff et al. 12797). Compound botryoids occur in *Eusideroxylon zwageri* (O. Beccari 2611).

Thyrsoids are especially common in Cryptocaryeae. Thyrsoids with three-flowered cymes are present in *Beilschmiedia moratii* (van der Werff 1996), *Beilschmiedia tawa* (H. Travers s.n.), *Cryptocarya alba* (G. Geisse s.n., 1912), *Cryptocarya gracilis* (Kostermans 1974*a*; G. McPherson 6244), *Cryptocarya mackeei* (Kostermans 1974*a*), *Cryptocarya odorata* (G. McPherson 5176), and *Endiandra hypotephra* (S. Kajewski 1443). Thyrsoids with five- to seven-flowered cymes are present in *Cryptocarya leptospermoides*; thyrsoids with three- to seven-flowered cymes seem to be present in *Cryptocarya aristata* (Kostermans 1974*a*).

Also in compound thyrsoids, three-flowered cymes are common, such as in *B. tawa* (D. Petrie, s.n., s.d.), *Beilschmiedia crassa*, and *Beilschmiedia microcarpa* (Nishida 2006); *Endiandra neocaledonica* (Kostermans 1974*a*); *Cryptocarya impressa* (Griffith s.n., 1863–4); *Cryptocarya microneura* (J. Canfield s.n., 1897); and *Cryptocarya laurifolia* (C. Wenzel 2861).

*Beilschmiedia novae-britanniae* has compound thyrses or thyrsoids (?; Kostermans 1970*a*). *Cryptocarya velutinosa* has thyrses (without a terminal flower?) with dichasial cymes composed of two triads but without a first-order flower (Kostermans 1974*a*; also *Cryptocarya myrtifolia*, C. Schröter, s.n., 30 X 1926).

1. Ramification is commonly of the first or also of the second order but goes up to the third order in *Beilschmiedia* and in *Endiandra* even more: 0–1 order in *Dahlgrenodendron*, having single flowers or triads (van der Merwe et al. 1988; Kostermans 1990); 1 order in *Beilschmiedia tirunelvelica* (Manickam et al. 2005); 1–2 in *Endiandra* (Kostermans 1974*a*; Hyland 1989); 4 in *B. minutiflora* (G. Zenker 1695), *Endiandra cowleyana* (P. Forster 28151), and *Eusideroxylon zwageri* (O. Beccari 2611); 4–5 in *Beilschmiedia recurva* (P. Forster 28167) and *Endiandra bessaphila* (P. Forster 28166). Other species of *Endiandra* may have an even richer branching system with higher axial orders (Arifiani 2001): up to 5 in *Potameia thouarsii* (S. Totozafy Be STB 548) and in *C. odorata* (M. Balansa 1848).

2. In *Cryptocarya aschersoniana* (G. Hatschbach 55766), the leaves are alternate; however, inflorescence branches are at least partly opposite. New Caledonian *Endiandra* species have opposite or alternate flowers, and *Cryptocarya* species have alternate flowers (according to illustrations in Kostermans 1974*a*). Flowers in thyrsoids, with triads as modules (also terminal triad), 1 (first-order branching) alternate, 2 (second-order branching) opposite: *C. aschersoniana* and *Endlicheria paniculata* (de Vattimo 1979), also in *C. gracilis* (G. McPherson 6244). Thyrsoid with triads: 1, 2 (first and second order) branching, opposite: *B. moratii* (van der Werff 1996). Thyrsoid with triads, pentads, and heptads as lateral units: 1, 2 opposite: *Cryptocarya rubra* (Kostermans 1937); thyrsoid: 1 alternate, 2 opposite: *E. hypotephra* (S.F. Kajewski 1443); thyrsoid: 1, 2 opposite: *C. alba* (G. Geisse s.n., 1912); compound botryoid: 1, 2, 3 alternate: *B. minutiflora* (G. Zenker 1695); compound botryoid: 1, 2, 3 alternate: *Beilschmiedia mannii* (W. de Wilde 304); compound botryoid: 1, 2 alternate: *Beilschmiedia diversiflora* (M. Le Testu 8099); compound botryoid: 1, 2, 3, 4, 5 alternate: *Potameia thouarsii* (S.Totozafy Be STB 548); compound botryoid: 1 alternate, 2 alternate or opposite-alternate, 3 alternate: *P. micrantha* (H. van der Werff et al. 12777); compound botryoid: 1, 2, 3 alternate, 4 opposite: *E. zwageri* (O. Beccari 2611); compound thyrsoid: 1, 2, 3 alternate: *B. recurva* (P. Forster 28167); thyrsoid or compound thyrsoid: 1, 2 alternate, 3, 4, 5, opposite: *C. odorata* (M. Balansa 1848); compound thyrsoid: 1, 2 alternate, 3 opposite: *C. impressa* (East India Company 4277), and *C. laurifolia* (C. Wenzel 2861). Compound thyrsoid: 1, 2 alternate, 3, 4 opposite: *E. bessaphila* (P. Forster 28166); compound thyrsoid: 1 almost opposite, 2, 3 opposite *Beilschmiedia tawaroa* (Wright 1984); compound thyrsoid with triads, pentads, heptads: 1, 2 alternate, 3 alternate or opposite, 4 opposite: *B. tawa* (D. Petrie s.n., s.d.).

3. Symmetry of branching: triads (symmetric) or pentads (asymmetric) in *C. rubra* (Kostermans 1937); triads (symmetric) in *Cryptocarya aschersoniana* (de Vattimo 1979); triads (symmetric) and dyads (asymmetric) in *C. laurifolia* (C. Wenzel 2861).

4. Prophylls in outermost lateral branches are present in *E. neocaledonica* (Kostermans 1974*a*).

5. Position of prophylls unknown.

6. Occurrence of metaxyphylls unknown.

7. Metatopies were found in *Endiandra baillonii*, in which the subtending bracts of the lateral flowers of part of the triads in the thyrsoids were fused with the pedicel (G. McPherson 5176). Metatopies are perhaps also present in *C. mackeei* (Kostermans 1974*a*); in *E. sebertii* and *E. poueboensis* floral subtending bracts seem to be higher, on the lateral branch (Kostermans 1974*a*). In *C. alba* (G. Geisse s.n., 1912) the subtending bracts of the lateral flowers of the triads are higher on the pedicel of the flowers. In *C. gracilis* this is true for the two distal triads (G. MCPherson 6244, PTBG). In *P. micrantha* the subtending bracts of the branches that branch from the second-order branches are slightly displaced upward on the third-order branches (H. van der Werff et al. 12777).

8. An accessory inflorescence branch was found abaxially in *C. odorata* (G. McPherson 4283).

9. Ramiflory and cauliflory appear not to be recorded.

10. Only rarely are floral bracts not caducous: perhaps partly in *P. micrantha* (H. van der Werff et al. 12777).

11. A long stalk is not present in *E. zwageri* (O. Beccari 2611) and *C. rubra* (Kostermans 1937).

**Lauraceae–the "Large Clade": Core Lauraceae and Mezilaurus Group (according to Rohwer and Rudolph 2005).** *Ocotea gabonensis* has botryoids of three to five or more flowers (Fouilloy 1965), *Ocotea tsaratananensis* with ca. 10 flowers (van der Werff 1996). *Machilus holadenia* has botryoids with five to seven flowers (Ho 1932), *Cinnamomum archboldianum* with five to seven flowers (Kostermans 1986), *C. burmanni* with three to seven flowers (P. Endress 03-68), *C. gracillimum* with seven flowers (Kostermans 1986), and *Ocotea botrantha* with 10–17 flowers (P. Endress 1118). Botryoids also occur in *Nectandra filiflora* (Rohwer 1993*b*). In *Pleurothyrium* botryoids, thyrsoids, and possibly also compound thyrsoids occur (van der Werff 1993).

Compound botryoids are present in *Alseodaphne* sp. (W. de Wilde & B. de Wilde-Duyfjes 13919) and in (male) *Gamanthera* (van der Werff and Endress 1991), *Ocotea bullata* (five flowers in a botryoid; Forest Officer, Transkai CC 886), *Ocotea bicolor*

(five flowers in a botryoid; G. Hatschbach 50096), and *Ocotea amazonica* (probably up to nine flowers in a botryoid; B.M. Boom & A.L. Weitzman 5251).

Thyrsoids with three-flowered cymes are present in *C. ebaloi*, *C. englerianum*, *C. novae-britanniae*, *C. ledermannii*, *C. pilosum*, *C. piniodorum*, *C. roesselianum*, *C. sessilifolium*, *C. trichophyllum*, *C. xanthoneurum* (Kostermans 1986), *C. verum* (as *C. zeylanicum*; Fouilloy 1965), *Aiouea acarodomatifera* (R. Klein 1659), *Nectandra apiculata* (Rohwer 1993*b*), *Ocotea oligantha* (van der Werff 1996), *Persea americana* (Pax 1889*a*), or compound thyrsi of thyrsoids. *Aniba lancifolia* has thyrsoids with triads or dyads (Kubitzki and Renner 1982).

Thyrsoids with three- to five-flowered cymes are present in *Ocotea sambiranensis* (van der Werff 1996). Thyrsoids with three- to seven-flowered cymes occur in *C. verum* (F. Fosberg 60444, PTBG; Pax 1889*a*; Kostermans 1986), *Nectandra cerifolia* (Rohwer 1993*b*), *Nectandra oppositifolia* (Y. Mexia 4461), *Ocotea aurantiodora* (Kurz 2000), and *Persea hexanthera* and *Persea nivea* (Kopp 1966). Thyrsoids with three- to seven- or more-flowered cymes occur in *Persea cuneata* (Kopp 1966) and *Rhodostemonodaphne* (Madriñán 1996). Often the cymose units of the thyrsoids have five to seven flowers, such as in *C. camphora* (P. Endress 2605) and *C. tahijanum* (Kostermans 1970*b*). Thyrsoids with seven-flowered cymes occur in *Nectandra membranacea* (C. Cid Ferreira et al. 10536).

In *Aniba pedicellata* the cymes of the thyrsoids have even more flowers (with branching up to the fourth order; Kubitzki and Renner 1982). Thyrsoids with up to 31 flowers in a cyme (cyme with four branching orders) were found in *Nectandra cuspidata* (G. Hatschbach 5804). Thyrsoids with cymes up to five times branched are mentioned for *Nectandra angusta* (Rohwer 1993*b*).

Thyrsoids with only two cymes, branched (two), three, or four times occur in *Nectandra egensis* (Rohwer 1993*b*). This is similar to *Hypodaphnis*.

Compound thyrsoids occur in *Aiouea lehmannii* (Kubitzki and Renner 1982), *Aiouea tomentella* (Kubitzki and Renner 1982), *Aniba firmula* (de Vattimo 1979), *Aniba desertorum* (Kubitzki and Renner 1982), *Caryodaphnopsis theobromifolia* (van der Werff and Richter 1985), *Cinnamomum myrianthum*, *C. polderi*, and *C. rosselianum* (all three-flowered cymes; Kostermans 1986), *C. solomonense* (ca. seven-flowered cymes; Kostermans 1986), *C. sleumeri* (7- to 15-flowered cymes; Kostermans 1970*a*, 1986), *N. membranacea* (P. Sintenis 4656), *Ocotea grayi* and *Ocotea malcomberi* (three-flowered cymes), *Potameia micrantha* (three- and more?-flowered cymes; van der Werff 1996), *Ocotea dentata* (three- to seven-flowered cymes; Burger and van der Werff 1990), *Ocotea aciphylla* (three-flowered lateral units; G. Hatschbach 54799), and *Persea silvatica* (three- to seven-flowered cymes; Burger and van der Werff 1990). In *Persea americana* several thyrsoids with three-flowered cymes are arranged in a compound thyrse (Buzgo et al. 2007). Whether simple thyrses (i.e., without terminal flowers) occur in Lauraceae at all, as the illustration of *C. cebuense* (four-flowered cymes) in Kostermans (1986) suggests, should be critically studied with live material.

According to Kurz (2000) *Aniba panurensis* has panicles. However, these inflorescences can also be described as compound botryoids, each botryoid with two to six flowers (J. Ramos 1857). *Clinostemon* sp. has compound racemes (without terminal flowers; Kurz 2000).

The parasitic winding genus *Cassytha* has simple spikes or racemes (Mez 1889; Weberling 1985); *Cassytha* is sister to the remaining Lauraceae (minus *Hypodaphnis* and Cryptocaryeae; Song et al. 2017). Racemes also occur in *Mezilaurus*.

The highly nested tribe Laureae (Li et al. 2004) of the large clade is characterized by botryoids with congested flowers, the floral bracts forming an involucre. Thus, *Litsea* and *Laurus* have botryoids of often five flowers (Mez 1889; Kasapligil 1951). If an involucre surrounds more than five flowers in *Litsea*, the lower branches may be triads instead of single flowers (Ruge 2000).

Within Laureae evolutionary simplifications have led several times to inflorescences consisting of single flowers that are preceded by numerous (several) empty bracts, as present in *Dodecadenia* (Pax 1889*a*; Weberling 1985; Rohwer 1993*a*), *Iteadaphne* (Pax 1889*a*; Rohwer 1993*a*), and *Litsea deplanchei* (Kostermans 1974*a*). In addition, flowers in *Lindera* and *Litsea* are unisexual, and a number of species have lost their perianth (Hyland 1989; Endress 1990).

1. Branching orders in inflorescences: often 3 but up to 4 in *A. desertorum* and *A. pedicellata* (Kubitzki and Renner 1982), *A. panurensis* (Kurz 2000), *O. dentata* (Burger and van der Werff 1990), *Triadodaphne myristicoides* (Kostermans 1974*b*), 4–5 in *N. cuspidata* (G. Hatschbach 58604) and *N. angusta* (Rohwer 1993*b*).

2. Triads in thyrsoids are opposite or alternate in *P. americana* (Stout 1927); although leaf phyllotaxis is alternate, dichasia in other *Persea* species are mostly alternate (Kopp 1966), but branches of the last triad are mostly opposite (J. Rohwer, personal communication). Flowers in botryoids are more or less opposite in *M. holadena*, and vegetative leaves are subopposite (Ho 1932). Leaves and flowers (in botryoids) are opposite in *C. archboldianum* and *C. gracillimum* (Kostermans 1986); botryoid: alternate, distally opposite in *N. filiflora* (Rohwer 1993*b*); flowers in thyrses, with triads as modules (either single triads or dichasia of two triads), alternate in *Phoebe kwangsiensis* (Ho 1932). In *Licaria reitzkleiniana* the two lateral flowers of a triad are opposite, and triads are opposite each other (de Vattimo 1979). Lateral branches of the thyrsoids are more or less opposite (triads?) in *Ocotea racemosa* (Kostermans 1950). In *Pleurothyrium* the inflorescence branches (single flowers or cymes) are opposite or alternate (van der Werff 1993). Thyrsoid: 1 (first branching order) alternate, distally opposite, 2 (second branching order) opposite in *N. apiculata* (Rohwer 1993*b*); thyrsoid: 1 alternate, 2 or 2, 3 opposite in *N. cerifera* (Rohwer 1993*b*); thyrsoid: 1 alternate, 2, 3 opposite in *C. camphora* (P. Endress 2605), *N. membranacea* (C. Cid Ferreira et al. 10536), and *Aiouea saligna* (G. Prance & N. Silva 58606); thyrsoid: 1, 2, 3, 4, 5 opposite in *N. egensis* (Rohwer 1993*b*); compound botryoid: alternate (except terminal triad) on main and lateral botryoids: *Alseodaphne* sp. (W. de Wilde & B. de Wilde-Duyfjes 13919); 1 alternate, 2 opposite: *A. acarodomatifera* (R. Klein 1659); 1 alternate, 2, 3, 4, 5 opposite: *N. cuspidata* (G. Hatschbach 58604); 1 alternate, 2 alternate or alternate-opposite, 3 alternate, 4 opposite; 1, 2 alternate (compound botryoids): *O. bicolor* (G. Hatschbach 48235, 50096); 1 alternate, 2 alternate or opposite: *O. amazonica* (B. Boom & A. Weitzman 5251).

3. Symmetry of branching: commonly symmetric: 1, 2 *C. verum* (F. Fosberg 60444); dyads (asymmetric) in *A. lancifolia* (Kubitzki and Renner 1982; whether one flower fallen?).

4. Prophylls in the outermost branches are often present, at least partly in *C. camphora* (P. Endress 2605), *C. burmanni* (P. Endress 03-68), and *N. membranacea* (C. Cid Ferreira et al. 10536).

5. Position of prophylls: basal: *C. burmanni* (P. Endress 03-68), *A. saligna* (G. Prance & N. Silva 58606), and *O. botrantha* (P. Endress 1118).

6. Empty bracts below terminal flower (metaxyphylls) in botryoids are present in *Pleurothyrium golfodulcense* (van der Werff 1993) and *C. burmanni* (P. Endress 03-68).

7. Metatopies were not found.

8. Accessory flowers appear to have been largely neglected in the literature on Lauraceae. Accessory flowers or buds at the base of inflorescences are mentioned for *Litsea glaucescens* and *Cassytha* (Mez 1889) and for *Beilschmiedia*, *Laurus*, and *Lindera* (Weberling 1985). However, according to our studies, accessory flowers do not appear to be common in Lauraceae. In our material, *A. saligna* (G. Prance & N. Silva 58606) has thyrsoids, and some of the lateral cymes are accompanied by a basal abaxial branch that may be an accessory branch. In *O. bicolor* (G. Hatschbach 50096) some of the botryoids in the compound botryoids are accompanied by a basal abaxial flower or triad that may be accessory branches.

9. Ramiflory and cauliflory are rare. Ramiflory is present, for example, in *Litsea* p.p. (Kostermans 1970*a*; Hyland 1989). Cauliflory is present in *Litsea ripidion* (Kostermans 1974*a*).

10. Floral bracts in derived Lauraceae tend to be early caducous (Mez 1889; Weberling 1985; this study). They are commonly no longer present at anthesis. Only in few taxa are floral bracts not caducous (*Phoebe semecarpifolia*: Mez 1889; some *Pleurothyrium* species: van der Werff 1993). However, involucral bracts are probably more persistent (e.g., *Laurus*, *Litsea*, *Lindera*; e.g., Kostermans 1957, 1974*a*; Hyland 1989). For involucres, see Weberling (1985, 1988) and Rohwer (1993*a*).

11. A long stalk is often present.

**Lauraceae–Fossil.** The fossil Cretaceous (Cenomanian) *Mauldinia mirabilis* from the Potomac Group (Cenomanian; Drinnan et al. 1990) and *Mauldinia bohemica* from Bohemia (central Europe; Eklund and Kvacek 1998) have thyrses of an elaborate kind. Their cymose units are dichasial-monochasial systems. In this branching pattern they resemble the genera *Siparuna* (Siparunaceae) and *Illigera* (Hernandiaceae). We are not aware of any extant Lauraceae with pronounced monochasial parts in the cymes of the thyrsoids. Additional Mid- to Late Cretaceous *Mauldinia* species with apparently cymose lateral inflorescence units were described from other localities in North America (Herendeen et al. 1999; Friis et al. 2006), Europe (Viehofen et al. 2008), and Kazakhstan (Frumin et al. 2004). *Pragocladus* (Cenomanian) also has compound inflorescences with an elongate main axis and several lateral axes with two to four flowers of unknown ramification pattern (Kvacek and Eklund 2003). Another unnamed Cretaceous (Santonian–Campanian) lauraceous fossil from North Carolina probably has triads as partial inflorescences (Eklund 2000). Middle Eocene Princeton Chert fossils appear to have thyrses (thyrsoids?) with triads as cymose units (Little and Stockey 2006).

### *Hernandiaceae*

The inflorescences are thyrses or compound thyrses (Kubitzki 1969; not stated whether there are also thyrsoids). In *Hernandia* the cymose units of the thyrses are three-flowered monochasia with unisexual flowers; their developmental sequence is male-male-female (Kubitzki 1969; Endress and Lorence 2004). In *Hazomalania* the plants are dioecious; male thyrses have three-flowered cymes (as in *Hernandia*) and female thyrses one-flowered units (Capuron 1966). Each monochasium has four relatively large involucral bracts (Kubitzki 1969; Endress and Lorence 2004), commonly still present at anthesis.

In *Illigera* the inflorescences are thyrses, and in the cymes the first branching is dichasial, followed by monochasia. The primary axis does not have a terminal flower; all flowers are bisexual (Kubitzki 1969).

In *Gyrocarpus* the inflorescences are compound thyrses or thyrsoids (?) that are highly branched (with branches up to order 10). Lower-order lateral branches lack terminal flowers; some of the terminal flowers of the higher-order lateral branches are bisexual, whereas the other flowers are male (Kubitzki 1969). The dichasia may also be regarded as thyrses with only two first-order lateral branches.

*Sparattanthelium* resembles *Gyrocarpus* in inflorescence structure, with branches of up to order 13; the flowers are bisexual (or polygamous?; Kubitzki 1969).

1. Branching orders are diverse: in *Hernandia* 3–5 (Kubitzki 1969), in *Illigera* ca. 6, in *Gyrocarpus* ca. 6–9, in *Sparattanthelium* ca. 8–12 (Kubitzki 1969).

2. Branching is alternate in all branching orders in *Hernandia*, almost opposite in the second order in *Illigera*, and opposite throughout *Gyrocarpus* (Kubitzki 1969) and *Hernandia nymphaeifolia* (Endress and Lorence 2004).

3. Branching is asymmetric in *Hernandia*, it is symmetric in the second branching order in *Illigera* but otherwise asymmetric, and it is symmetric in *Gyrocarpus* (Kubitzki 1969).

4. Prophylls are present in the outermost branches in *Hernandia* (Kubitzki 1969; Endress and Lorence 2004).

5. Prophylls are distal in *Hernandia* (Kubitzki 1969; Endress and Lorence 2004).

6. Not applicable, as there are no botryoids.

7. Metatopies are present in *Gyrocarpus* and in one species of *Illigera*. The subtending floral bracts are some distance away from the main inflorescence axis and appear fused with the lateral axis they subtend (Kubitzki 1969).

8. Accessory flowers were not reported (Kubitzki 1969; Endress and Lorence 2004).

9. Ramiflory or cauliflory were not found.

10. Floral bracts are usually persistent up to anthesis in *Hernandia* (Endress and Lorence 2004), caducous in *Sparattanthelium* (Kubitzki 1969), and mostly lacking in *Gyrocarpus* (Kubitzki 1969).

11. Long stalks are present in all genera (including *Hazomalania*; Kubitzki 1969).

## Discussion

How can inflorescences in Laurales be described most easily and meaningfully to be used for systematic comparisons at the level of the order and especially those with small and numerous flowers: Hernandiaceae, Lauraceae, Monimiaceae, and Siparunaceae? We usually follow the terminology of Weberling (1989) and Endress (2010), with some specifications that are useful within the order Laurales. Van der Werff and Richter (1996) and van der Werff (2001) also use inflorescence features in the classification of Lauraceae but without clearly defining them.

The most common inflorescence patterns in Laurales are botryoids (i.e., racemes with a terminal flower) and thyrsoids (i.e., thyrses with a terminal flower). In thyrsoids the branches (units) of the second branching order are often triads (three-flowered cymes). From this pattern there are two possibilities of further enrichment (this does not imply evolutionary directions): either by replacement of triads by botryoids, leading to compound botryoids (e.g., *Persea americana*; Fouilloy 1965) or by replacement of triads by further-branched cymes (e.g., heptads, leading to richer thyrsoids, e.g., *Rhodostemonodaphne elephantopus*; Madriñán 1996). Botryoids of five or more flowers mainly occur in Gomortegaceae, some Atherospermataceae, many Monimiaceae, and many Lauraceae. Dichasial triads mainly occur in Calycanthaceae, Gomortegaceae, some Atherospermataceae, some Monimiaceae, and Lauraceae.

In which groups are there single flowers? They occur in some Calycanthaceae, some Atherospermataceae, some Monimiaceae–Mollinedioideae, and rarely in Lauraceae (Laureae). Repeatedly found were one-flowered inflorescences, with the flower preceded by a larger number of bracts (*Chimonanthus praecox* in Calycanthaceae, *Hedycarya perbracteolata* and *Tambourissa cocottensis* in Monimiaceae, and *Dodecadenia* [Weberling 1985] and *Iteadaphne* and some *Litsea* species in Lauraceae and others).

The largest flowers of Laurales occur in such one-flowered inflorescences, in the apparently highly derived genus *Tambourissa* of Monimiaceae (Endress and Lorence 1983; Lorence 1985; Endress 1987*b*). In *Tambourissa ficus* the male flowers reach 7.5 cm in diameter (Lorence 1985).

The main patterns of inflorescences at the order level are as follows:

1. Number of branching orders commonly not more than one (or two) in clades 1 and 2 (except for Siparunaceae) and commonly two or more in clade 3 (clade 1 = Calycanthaceae; clade 2 = Atherospermataceae, Gomortegaceae, Siparunaceae; clade 3 = Hernandiaceae, Lauraceae, Monimiaceae; see the introduction).

2. Opposite or nonopposite branching (commonly opposite in clades 1 and 2 plus Monimiaceae). At least first branching commonly alternate in clade 3.

3. Symmetry of branching (in most cases symmetric; not well applicable at the order level).

4. Prophylls in the outermost branches are present in clades 1 and 2 (Siparunaceae uncertain); clade 3: Monimioideae uncertain but mostly absent in Mollinedioideae. Among Lauraceae present in Cryptocaryeae, uncertain in the other clades of the family; present in *Hernandia* of Hernandiaceae.

5. Position of prophylls (not well applicable at the order level).

6. Metaxyphylls in botryoids are common in clade 1 (Calycanthaceae) and clade 2 (Gomortegaceae, some Atherospermataceae; not applicable for Siparunaceae) and also in clade 3 (Monimiaceae) but uncertain or not applicable in Lauraceae and Hernandiaceae.

7. Metatopies with the subtending floral bracts lower or higher than the branching point are lacking in clades 1 and 2 (except Siparunaceae) but are present in clade 3 (Monimiaceae, except *Hortonia*, Lauraceae except for the large clade, Hernandiaceae).

8. Accessory flowers or inflorescence branches are absent in clade 1, present within clade 2 only in Atherospermataceae (*Daphnandra*, *Doryphora*), and present in clade 3 in many Monimiaceae, very few Lauraceae, and absent in Hernandiaceae.

9. Ramiflory or cauliflory are absent in clade 1, among clade 2 present in Siparunaceae, and among clade 3 in Monimiaceae and only a few Lauraceae.

10. Floral bracts are early caducous in clade 1, among clade 2 in Gomortegaceae and Siparunaceae (but often persistent in Atherospermataceae), and among clade 3 in Monimioideae–Monimiaceae, more or less in Cryptocaryeae, and the large remainder of Lauraceae mixed in Hernandiaceae.

11. Long stalks (hypopodia) at the base of inflorescence or second-order inflorescence branches, as compared with the following internodes, are lacking in clades 1 and 2 but are present in clade 3.

A shared tendency of Lauraceae and Hernandiaceae is to form a kind of involucre of bracts including several flowers. In *Hernandia*, this involucre of bracts surrounds a monochasium (according to Kubitzki 1969; Weberling 1988). This was supported by developmental studies (Endress and Lorence 2004). In Lauraceae (*Litsea*) the involucre surrounds a botryoid (Weberling 1985, 1988; Robi et al. 2015) or sometimes a thyrsoid (Ruge 2000). The Cretaceous *Mauldinia* (Lauraceae) appears to have dichasial-monochasial branching of the lateral cymes (Eklund and Kvacek 1998; Friis et al. 2006) that also occurs in *Illigera* (Hernandiaceae).

Three other families, Amborellaceae, Trimeniaceae, and Chloranthaceae, were earlier also included in Laurales or thought to be related to them. Amborellaceae and Trimeniaceae have later been identified as members of the basalmost angiosperms, the ANITA grade (Qiu et al. 1999, 2005; Renner 1999; APG IV 2016), and Chloranthaceae still have an uncertain position in basal angiosperms (Soltis et al. 2018). However, they may be sister to all other angiosperms above the ANITA grade (Doyle and Endress 2000, 2018; Qiu 2005; Mathews 2006). The inflorescence structure of these three families should also be briefly discussed and compared with that of Laurales.

*Amborella* (Amborellaceae; formerly included in Monimiaceae) has botryoids (or thyrsoids or compound botryoids) with accessory flowers (Endress and Igersheim 2000; Posluszny and Tomlinson 2003). Thus, it behaves as many Atherospermataceae and Monimiaceae (also Calycanthaceae?) in this respect. There are no panicles in *Amborella* (Endress and Igersheim 2000; Posluszny and Tomlinson 2003; as opposed to Weberling 1988, i.e., primary lateral branches never have more than two secondary lateral branches). Buzgo et al. (2004) mention branches of higher orders. However, they do not consider the presence of accessory flowers. Accessory flowers may give the false impression of higher-order branching.

Trimeniaceae (formerly also included in Monimiaceae) have botryoids or compound botryoids (Endress and Sampson 1983). Simple botryoids were found in *Piptocalyx moorei* (P. Endress 4005, Z) and *Trimenia neocaledonica* (G. McPherson 4044, Z), and compound botryoids with accessory flowers were found in *T. papuana* (P. Endress 4087, Z) and *T. weinmanniifolia* (Siwatibau s.n., 1971, Z). Small adaxial accessory botryoids were found in *T. papuana* (P. Endress 4087, Z; J. Womersley s.n., 1970, Z). Rarely in a botryoid the lowermost flower has a lateral flower in the axil of a prophyll (seen in *T. papuana* and *T. weinmanniifolia*). The lateral flowers in a botryoid are almost always in pairs; rarely some are slightly offset. Paniculate inflorescences were erroneously mentioned for *T. papuana* in Endress and

Sampson (1983). Chloranthaceae have compound racemes (*Chloranthus*, *Sarcandra*, *Ascarina*, male *Hedyosmum*) or compound thyrses (*Ascarina* p.p., female *Hedyosmum*; Endress 1987*a*; von Balthazar and Endress 1999; Kong et al. 2002).

## Conclusions

Botryoids and thyrsoids are most common in Laurales, whereas panicles are almost lacking. At the genus and species level the degree of ramification in the cymose partial inflorescences of the thyrsoids is of interest, as its extent may be different from species to species within a genus or family.

Thus, in conclusion, "pure, classical" panicles are not or are rarely present in Laurales. Kurz (2000) mentions panicles for *Aniba panurensis* of Lauraceae. However, they can also be seen as compound botryoids, as the increase of branching along the main inflorescence axis toward its base is not continuous—in contrast to classical panicles—but staggered. That panicles are rare may even be true for basal angiosperms in general. The same may be the case for thyrses.

In general, smaller units (modules) are more interesting to consider than entire inflorescences for our purpose. They are more stable units at the mesolevel (genera and families) than entire inflorescences in Laurales.

## Acknowledgments

For support in the field P. K. Endress thanks Bernie Hyland (Atherton). We thank Susanne S. Renner (Munich) and Yannick M. Staedler (Vienna) for unpublished information on Calycanthaceae. We acknowledge Edwin Frey (Ronco), Werner Rauh (Heidelberg), and Tod Stuessy (Vienna) for plant material. We also thank the directors of the herbaria consulted (Conservatoire et jardin botaniques, Genève [G]; National Tropical Botanical Garden, Kauai [PTBG]; Herbaria of the University of Zurich [Z]; and ETH Zurich [ZT]). Alex Bernhard is acknowledged for support with the illustrations. For their very careful reviews of the manuscript we thank Jens Rohwer and Dmitry Sokoloff. Jens Rohwer also pointed to revised names of some old herbarium specimens and to an unpublished diploma thesis mentioned in the text, which we greatly acknowledge.

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